CO-EVOLUTION OF *CLAYTONIA VIRGINICA* (PORTULACACEAE) AND ITS MAIN NATIVE POLLINATOR, *ANDRENA ERIGENIAE* (ANDRENIDAE)

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Abstract.—Flowers of *Claytonia virginica* were open and bore pollen and nectar from about 0800 to 1900 hours; however, female *Andrena erigeniae* foraged from only about 0800 to 1500 hours. These females were most abundant on a mostly shady, west-facing slope when ambient temperature peaked and on a sunny, east-facing slope 2 hours before it peaked. They showed a preference for sunny and partly sunny flower patches on the east-facing slope but not on the west-facing slope. Foraging females tended to be in plots with the densest flowers. Day-1 ("male") flowers had pollen more frequently than older ("female") ones, but female flowers had nectar more often than males, perhaps increasing cross-pollination. Flowers showed heliotropism that should increase flower metabolism and help bees to warm up on cool days. Mean floral temperature was usually higher than ambient temperature, being significantly positively correlated with flower light reflectance in some cases.

Flowers and their pollinating animals show different degrees of co-adaptation (Proctor and Yeo, 1973). Particular species of insect-pollinated flowers are visited by from primarily one (Michener and Rettenmeyer, 1956; Linsley, 1958; Thorp, 1969) to many pollen- and nectar-foraging insect species (Barrows, 1976, 1980; Eickwort and Ginsberg, 1980) and, in many cases, floral morphology restricts the number and species of pollinators to those of certain sizes, with certain tongue lengths, or both (Proctor and Yeo, 1973). Bees that specialize on only one or a few flower species might be particularly efficient in obtaining provisions from those flowers (Eickwort and Ginsburg, 1980), as is true for the oligotropic bee *Hoplitis anthocopoides* (Schenck) and its host plant, *Echium vulgare* (Strickler Vinson, 1978). Moreover, oligotropic bees are temporally synchronized with their host flower behavior (Eickwort and Ginsberg, 1980).

Michener and Rettenmeyer (1956) remarked that some of the physical

factors that determine the activity periods of a solitary bee are a complex of interrelations between air temperature, soil temperature, wind, and light intensity. According to Linsley (1978), "the most important limitations imposed by entomophilous plants on patterns of bee visitation are times of flower opening and closing and anthesis and nectar production."

In an attempt to increase understanding of the co-evolution of oligotropic bees and their host flowers, we studied the spring ephemeral *Claytonia virginica* L. (Portulacaceae) and its principal pollinator in Washington, D.C., the bee, *Andrena erigeniae* Robertson (Andrenidae). Most *Andrena* species forage on spring ephemerals in forests before the tree canopy closes (Eickwort and Ginsberg, 1980). Schemske (1977) and Schemske et al. (1978) studied the floral biology of *C. virginica* in Illinois. Individual flowers last an average of 3 days (range 1–9). The anthers dehisce soon after the flower first opens in early morning. At this time and throughout day-1, the filaments adpress the style, the stigma is unreceptive, and the flower is functionally staminate. When the flower reopens on day-2, the filaments are rotated 90° away from the style and adpress the petals; also, the stigma splits longitudinally and becomes 3-cleft. The flowers are functionally pistillate for from 1 to 8 days; however, a few pollen grains are often found on or near anthers of pistillate flowers. The shallow, pentamerous, actinomorphic flowers of *C. virginica* are basically disk- to bowl-shaped when open; thus, many types of insects can collect their pollen and nectar. In Illinois, Schemske (1977) found that these flowers were visited by 23 species of insects, but he noted that *A. erigeniae* is the flower's primary native pollinator by virtue of its abundance and foraging behavior. This bee collects pollen only from and has the same geographic range as *C. virginica* (Davis and LaBerge, 1975).

In view of the mutualism between *C. virginica* and *A. erigeniae*, data were collected to determine: (1) Effective sexes of flowers that bear pollen and nectar; (2) when open flowers have these resources with respect to the foraging period of *A. erigeniae*; (3) *A. erigeniae* visitation rates to sunny, partly sunny, and shady patches of *C. virginica*; (4) possible heliotropism in this flower and possible relationships between (5) floral and ambient temperatures, (6) floral temperatures and light reflectance, (7) bee foraging periods and ambient temperature, and (8) bee forager frequency and floral density. Subjects 1–3 and 5–7 were studied on both an east-facing slope (EFS) and a west-facing slope (WFS); 4 and 8, only on the EFS.

Materials and Methods

Observations were made on an east-facing slope (EFS) from 10 to 23 April 1978 and a west-facing slope (WFS) on 10 and 11 May 1978 in a deciduous forest in Washington, D.C. (described by Barrows, 1978). On the EFS, a 100-m transect was established on the woodland floor where *C. virginica*
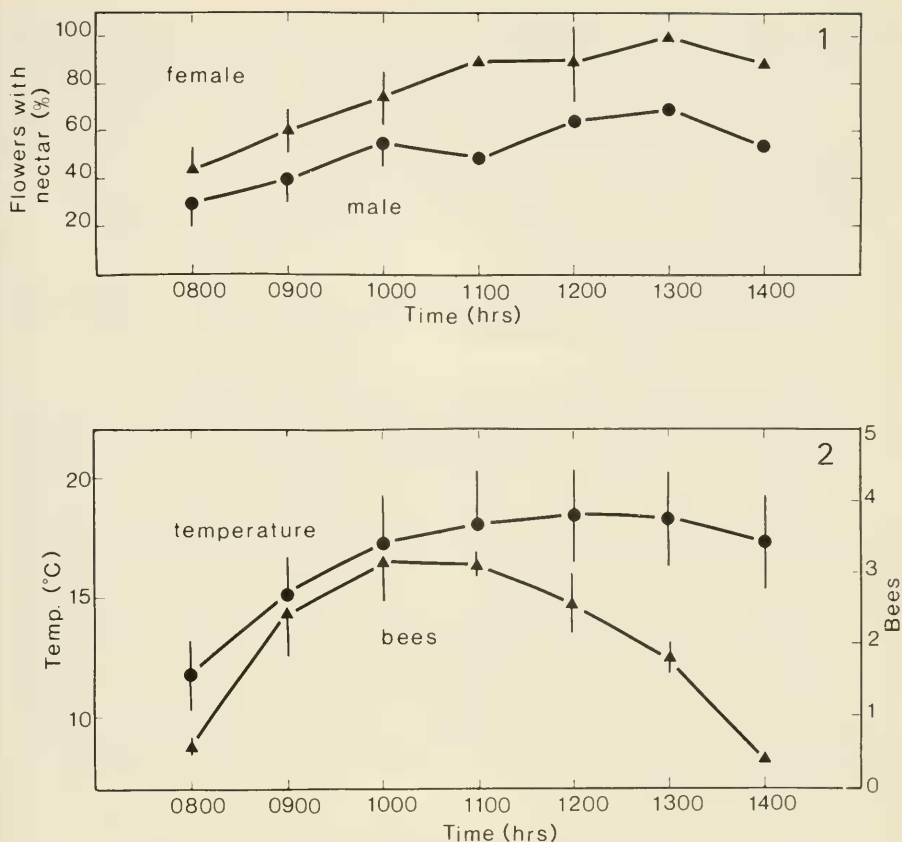
Fig. 1. Percentages of staminate (male) and pistillate (female) flowers with nectar on the EFS. Twenty flowers of each type were sampled at each time of the day. Standard errors of the means (SE) are indicated when they exceed symbol diameters.

Fig. 2.   Mean ambient temperatures and mean number of female bees foraging on the EFS on 10, 12, 14, 16, and 23 April. SE are indicated when they exceed symbol diameters.

were dense. Twenty 0.25 m^2 plots were randomly selected along the transect and marked off using twigs and string. By early May, only a few plants were in bloom on the EFS so the remaining observations were made on the WFS. Bees behaved differently on the EFS compared to the WFS; therefore, data from both slopes are presented below. On the WFS, 20 plots were established in the densest patches of *C. virginica*. Due to tree leaf development the WFS was more shaded than the EFS. Measurements were made only on sunny days in an attempt to make observations under physical conditions that were as similar as possible. Ambient temperature was recorded with a thermometer in the shade at 1 m above the ground. Female bees were

Table 1. Percentages of flowers with pollen and nectar. Each percentage is based on a sample of 140 flowers comprised of 20 different flowers that were sampled on the hour from 0800 to 1400 hours. A test for the equality of two percentages was used to analyze values.

	% Males	% Females	p
Flowers with Pollen			
East-facing slope	77.1	25.7	<0.001
West-facing slope	85.7	65.7	<0.001
Flowers with Nectar			
East-facing slope	52.1	78.6	<0.001
West-facing slope	13.6	25.0	0.015

counted during 30-s periods; male bees were not included in bee counts. Light reflectance of randomly selected flowers was measured with a Gossen Luna Pro® light meter with a Gossen Variable Angle Spot Meter Attachment®. Flower temperature was measured at insides of petal bases with a Bailey BAT-4 Biological Thermometer® and a BT-1 Thermometer Probe®. Presence of pollen and nectar droplets were detected with a 10× hand lens. Nectar was recorded as present if one or more droplets were seen. In the solar-tracking experiment, flower facing-direction was ascertained by aligning a lensatic compass with the longitudinal floral axis. The sun's position was determined with the compass from the shadow that a perpendicular nail cast on a horizontal plane. The abbreviation FT is used to indicate Fisher's exact probability test: KT, Kendall's ranked correlation test: WT, Wilcoxon's matched pair test.

Results and Discussion

Both 1-day (male, staminate) and older (female, pistillate) open flowers had nectar and pollen from about 0800 to 1900 hours and *A. erigeniae* foraged from about 0800 to 1500 hours (Fig. 1) on both the east-facing slope (EFS) and the west-facing slope (WFS). However, only a few pollen grains were present on or near anthers of female flowers. Male flowers had pollen significantly more frequently than females, and females had nectar more often than males (Table 1) on both slopes. This floral behavior may enhance cross-pollinating movements of bees. Schemske et al. (1978) point out that *C. virginica* is not an obligate outcrosser; however, cross-pollination could be important in the evolution of this flower. The flowers closed at night and during cool, overcast or rainy periods of the day.

The forager peak occurred later (1200 hours) on the WFS, compared to the EFS (1000 hours) (Fig. 2). Greater light intensity on the EFS probably caused this difference in bee activity because average morning ambient temperature from 0800 to 1200 hours was similar on the EFS and WFS, 16.0° and 16.8°C, respectively. As a result of different amounts of light impinging
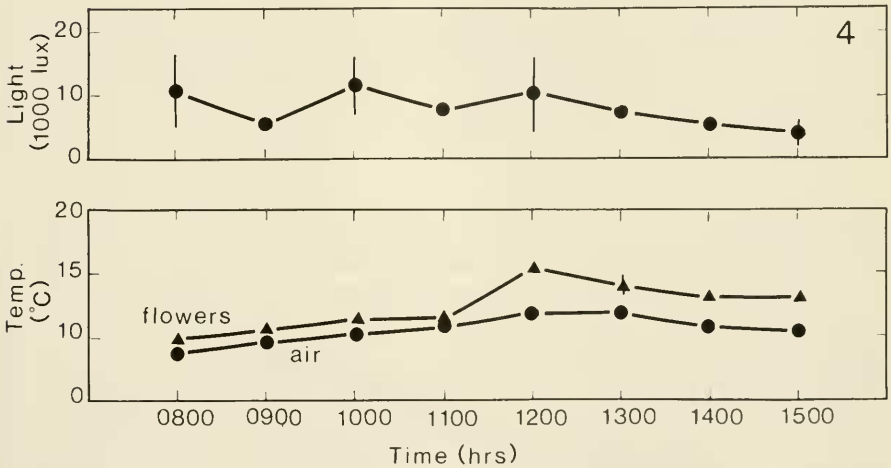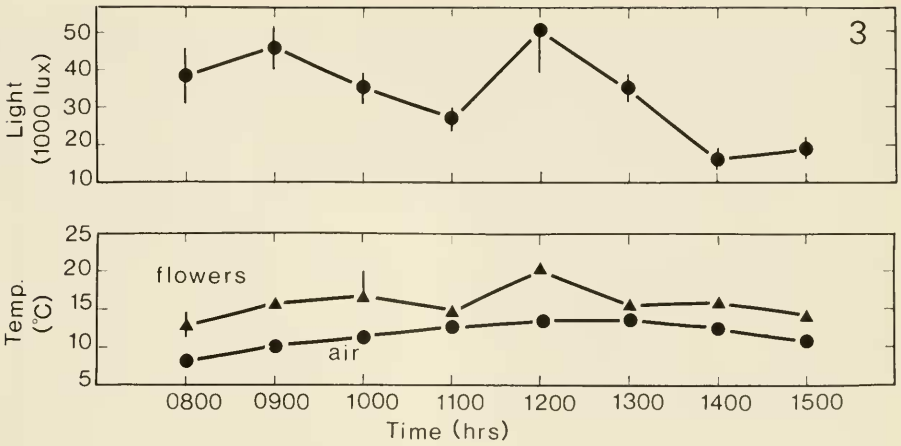
Fig. 3. Ambient temperature, mean flower temperatures, and mean amounts of light reflected from flowers in full sun on the EFS on 16 April. Each mean is based on 10 flowers. SE are indicated when they exceed symbol diameters.

Fig. 4. Ambient temperature, mean flower temperatures, and mean amounts of light reflected from flowers in shade on the EFS on 16 April. Each mean is based on 10 flowers. SE are indicated when they exceed symbol diameters.

on the slopes, flowers on the EFS reflected more light than those on the WFS. Ambient temperature, mean flower temperature, and mean amounts of light reflected by flowers in direct sun and in shade on the EFS are presented in Figs. 3 and 4.
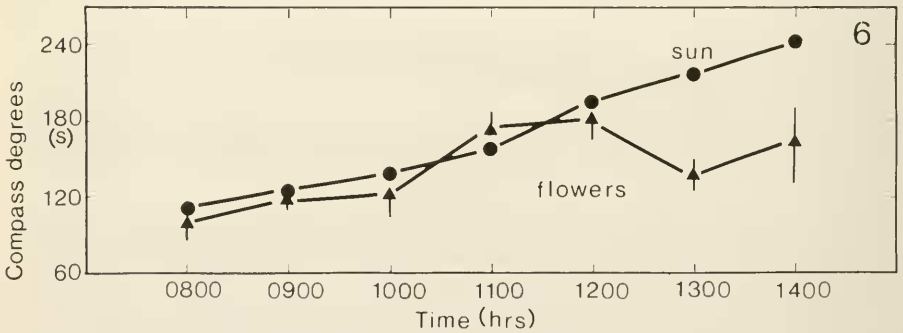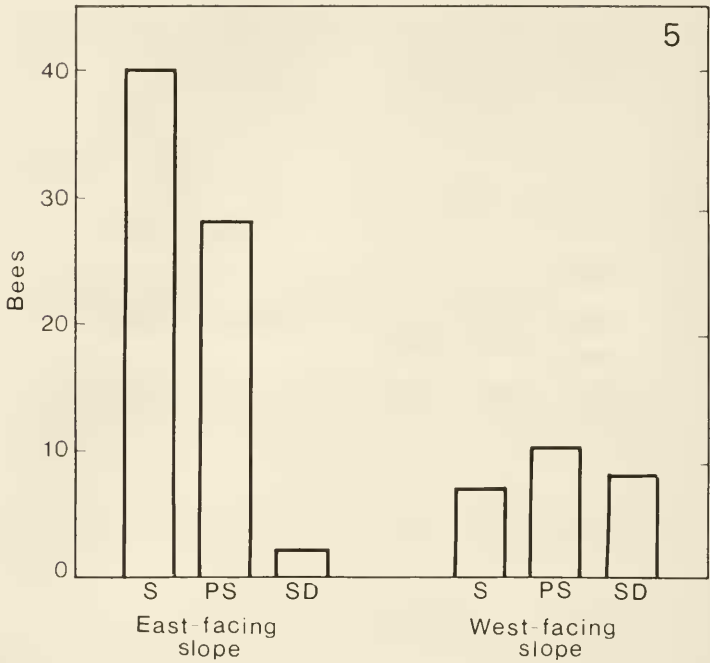
Fig. 5.   Numbers of female bees foraging in flower plots in full sun (S), partial shade (PS), and shade (SD) on both slopes. Five days of observations are combined for the EFS; 2 days for the WFS.

Fig. 6.   Flower facing directions and estimated position of the sun.

On clear days, *C. virginica* pollen and nectar were still available later than mid-afternoon (about 1500 hours) when most *A. erigeniae* stopped foraging. Thus the end of bee foraging at this time could be due to factors that we have not studied, such as their obtaining all the provisions that they needed for the day, insolation becoming too low for their being warm enough to forage, quantity of pollen being too low to be worth foraging costs, and quality, quantity, or both of nectar being too low.

On the EFS, more bees foraged in sunny and partially sunny plots and fewer bees foraged in shaded plots than would be expected by chance alone ($P < 0.001$, $P = 0.032$, $P < 0.001$, respectively, test for equality of two percentages, Fig. 5). On the WFS, 27% of the bees foraged in plots in direct sun; 41%, partial sun; 32%, shade. Their distribution was not significantly different from 33.3% in each type of plot ($P > 0.05$, Chi-square test for goodness of fit). The distribution of these foraging bees with regard to sunny, partially sunny, and shady flower patches is probably related to their thermoregulatory behavior. When ambient temperature is high enough, these bees might fly more under low light intensity. Linsley (1958) noted that cold weather, wind, and cloud cover significantly constrain foraging of small, solitary bees with relatively poor thermoregulatory capabilities. Käpylä (1974) concluded that temperature and light intensity were the most important weather factors controlling the flight activity of a mixed group of aculeate Hymenoptera in Finland. A quantitative study of flight energetics of *Andrena* has not been made.

Flower-facing directions were positively correlated with solar angular positions until 1200 hours on the EFS ($P = 0.021$, KT, Fig. 6), indicating that *C. virginica* flowers show heliotropism as in some other flowers (Kevan, 1975). After 1200 hours most of the flowers were no longer in direct sun (because the EFS had an inclination of about 45 degrees) and had stopped solar tracking. Heliotropism may increase the speed at which pollinators on flowers warm up and metabolize, and it can also increase floral metabolism resulting in increased nectar production and ovary development (Hocking, 1975; Kevan, 1975; Smith, 1975).

Mean flower temperature was usually higher than ambient temperature: EFS, flowers in shade ($P = 0.004$, WT), flowers in sun ($P = 0.004$); WFS, shade ($P > 0.05$), sun ($P = 0.031$) (Figs. 3 and 4). Some shade flower temperatures on the WFS were probably lower than ambient temperature due to evaporative cooling from transpiration; other flowers were probably warmer because they received enough insolation to warm up slightly, although their transpiration probably increased with temperature.

In shade flowers on the EFS, and in sun flowers on the WFS, mean flower temperature was positively correlated with ambient temperature 1 m above the ground ($P = 0.019$, 0.014, KT, respectively) (Burr, 1960). However,

Table 2. Mean numbers of flowers in plots that attracted and those that did not attract bees on the east-facing slope. Ranges and sample sizes of plots are given in parentheses.

	Number of Flowers	
Date (1978)	Plots With Bees (mean ± S.E.)	Plots Without Bees (mean ± S.E.)
12 Apr.	19.17 ± 4.001 (4–53, 12)	13.30 ± 4.402 (1–35, 8)
14 Apr.	43.46 ± 6.174 (9–94, 13)	18.57 ± 5.451 (5–38, 7)
15 Apr.	53.40 ± 6.097 (18–81, 10)	34.70 ± 8.149 (8–78, 10)
16 Apr.	51.0 ± 8.300 (29–79, 5)	40.27 ± 6.370 (8–86, 15)
23 Apr.	38.71 ± 12.115 (7–88, 7)	37.0 ± 4.798 (10–64, 13)

mean flower temperature of sun flowers on the EFS and shade flowers on the WFS was not correlated with ambient temperature on our sample days.

Mean flower temperature was positively correlated with their light reflectance on the WFS (shade flowers: $P = 0.038$, sun: $P = 0.014$, KT), but not on the EFS (shade and sun flowers: $P < 0.05$). Light intensity gradually increased over the shaded WFS and it markedly fluctuated over the less-shaded EFS due to cloud movements on our sampling days. More frequent sampling on the EFS probably would have revealed positive correlations between flower light reflectance and temperature.

Mean foraging bee density was not correlated with mean ambient temperature ($P > 0.05$, on both slopes, KT, Fig. 2). On the EFS, foraging female bees attained their highest densities 2 h before ambient temperature peaked and on the WFS they were most frequent when ambient temperature peaked at 1200 hours. The bees frequently basked when ambient temperature was low and light intensity was high; evidently, this enabled them to warm up enough to fly in cool air.

On 5 days on the EFS, plots that were visited by bees had a higher mean number of flowers than those that did not have bees during observation periods ($P = 0.004$, FT, Table 2), showing that the bees were drawn to areas of greater flower density. Open flowers were counted at 1100 hours. Waddington (1976) also observed that denser patches of flowers draw more bees than sparser patches.

In conclusion, heliotropic *C. virginica* flowers were open and had pollen and nectar on clear days from about 0800 to 1900 hours. Flowers tended to be warmer than the air above them. This should increase flower metabolism

and *A. erigeniae* temperature on cool, spring days. Most female *A. erigeniae* foraged from about 0900 to 1500 hours. Thus, although they are the main pollinators of *C. virginica*, their daily foraging period was shorter than the blooming period of this flower.

ACKNOWLEDGMENTS

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